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Feedback-dependence and robustness of gamma oscillations in networks with excitatory and inhibitory neurons

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Abstract

Synchronous rhythmic firing activity is fundamental tool for encoding and exchanging information in the brain. Based on inhibitory feedback neural network model, the network oscillations and the effect of the heterogeneity in the network on the oscillatory firing activity are studied. By using numerical simulations, global network oscillations in the gamma frequency band are obtained. The power of gamma oscillations is proportional to the inhibitory feedback gain. When the network model is heterogeneous, the gamma oscillations are robust with a moderate amount of heterogeneity. Stronger inhibitory feedback is beneficial to improve the robustness of the network oscillations against the heterogeneity. The network model in this paper can achieve robust gamma oscillations against a degree of heterogeneity, which is comparable to that observed in real neural systems.

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Keywords: Inhibitory feedback; gamma oscillation; power spectrum; heterogeneity

1. Instruction

A wide spectrum of spatially synchronous, rhythmic oscillatory patterns of activity have been observed in a variety of functional areas, including those involved in attention, audition, vision, and motor control [1-4]. Evidence has been presented that oscillations are critical for understanding sensory and cortical processing [5-7]. The mechanisms underlying oscillations and the influence of neural connectivity on

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these oscillations have been the subjects of intense research efforts in many studies [5,8,9]. In particular, it has been suggested that pyramidal neurons can be phase-locked to the field gamma oscillations, entraining by synchronous rhythmic inhibition originating from fast-spiking interneurons [10,11].

To investigate the gamma population oscillations, a network of excitatory and inhibitory neurons is adopted in numerical simulations. The pyramidal neurons are represented by the excitatory neurons, while inhibitory neurons correspond to the interneurons. Most theoretical and computational studies have investigated gamma oscillations of neural firing in homogeneous networks of excitatory and inhibitory neurons [12,13]. Generally speaking, the neural systems are heterogeneous. Dispersion in firing rates of neurons can be caused by heterogeneity [11]. It would be of interest to investigate whether the synchronous network oscillations may be robust in the presence of heterogeneities.In this paper, we focus on the generation and robustness of the synchronous oscillations described in several sensory systems, using numerical simulations in homogeneous and heterogeneous networks of excitatory and inhibitory neurons. The network model exhibits gamma oscillatory activity, which is robust when the network is exposed to a moderate amount of heterogeneity. We further explore the method to enhance the robustness of the gamma oscillations.

2. Model and numerical methods

In order to investigate the robustness of the gamma oscillations—the ability of the network to maintain synchronous oscillations in the presence of heterogeneities and noise—a network model consisting of two interacting layers of excitatory and inhibitory neurons with a time delay in the feedback loop is used for numerical simulations [12,13]. External input is provided to N_E excitatory neurons, which feed their output to an inhibitory neuron. In addition to the external input, the excitatory neurons receive feedback with gain G from the inhibitory neuron. Regarding the type of neurons, the leaky integrate-and-fire (LIF) model is an approximation of the physiological neuron, which is widely used in numerical simulations [5,8,12]. The dynamics of the membrane potential of LIF model is described as follows:

$$\tau_{\mathrm{m}} \frac{dV(t)}{dt} = E_{\mathrm{L}} - V(t) + R_{\mathrm{m}} I(t) , \tag{1}$$

where $V(t)$ is the membrane potential, $I(t)$ is the input current, E_L is the resting potential and R_m is the membrane resistance of the model. Here time is measured in units of the membrane time constant τ_m. Every time the membrane potential reaches the firing threshold V_T, the neuron fires and the membrane potential resets to a value V_R. After firing, the membrane potential is kept fixed for an absolute refractory period τ_R. Each excitatory neuron in the input layer receive an input:

$$I_i(t) = \mu + \sigma\left[\sqrt{1-c}\,\xi_i(t) + \sqrt{c}\,\xi_c(t)\right] - G\int_{\tau_D}^{\infty} \frac{t-\tau_D}{\tau_S^2} \exp\left[-\frac{t-\tau_D}{\tau_S}\right] \sum_j \delta(t-t_j)\, d\tau , \tag{2}$$

where τ_D is the transmission delay of the feedback loop, τ_S is the time constant of synaptic responses, and G is the feedback gain. The input consists of two noise processes $\xi_i(t)$ and $\xi_c(t)$, which are Gaussian low-pass filtered noise with zero mean and unit power. $\xi_i(t)$ is specific for each neuron and $\xi_c(t)$ is common to all neurons. The input correlation coefficient c determines the degree of correlation of the external input, while the total external input power remains σ.

With this network model, we can easily introduce the heterogeneity by setting homogeneous parameters diverse. In this paper, the inhibitory feedback gain G for each excitatory neuron is distributed according to Gaussian statistics with standard deviation σ_G. For both homogeneous and heterogeneous networks, each set of simulations is run with M realizations with time duration L to calculate the spike train power spectrum.

3. Results

We start by considering a simple case in which the inhibitory feedback gain is common for all individual excitatory neurons (i.e., without heterogeneity). Then the dependence of the oscillatory firing activity on the heterogeneity is studied. Using computer simulations, the results of numerical simulations for the spike train power spectrum of an excitatory neuron from the homogeneous network with delayed inhibitory feedback is compared to the heterogeneous case when $G=1$ in Fig.1(a). Since the statistics of firing activity are the same for all excitatory neurons, the power spectrum of the networks can be indicated by one neuron. For both cases (dashed line for homogeneous network or solid line for heterogeneous network), clear resonances near 50Hz are obtained due to the presence of global delayed inhibitory feedback and the correlated external input, which means the excitatory neurons oscillate in the gamma frequency band and the gamma oscillations is robust in the presence of heterogeneous feedback gain. Here σ_G=0.3 , which is used to measure the degree of the heterogeneity. The height of the peak for heterogeneous network is smaller than that for homogeneous network. Therefore, the heterogeneity in feedback loop produce asynchronous effect on the firing activity of the excitatory neurons.

The power of gamma oscillations can be quantified by the integral of the power spectrum from ω_1 to ω_2 [12]. Here $\omega_1=40$, $\omega_2=50$ .The shift in power of gamma oscillations with inhibitory feedback gain is described in Fig.1(b). A stable and relatively high level of $\Gamma_{40,50}$ is maintained with increases in G for homogeneous network, which is higher than that for heterogeneous network over the whole range of the values of G . The relatively flat and small values of $\Gamma_{40,50}$ for heterogeneous network imply that the heterogeneity in the feedback loop weakens the power of network oscillations. However, when σ_G is fixed at 0.3, $\Gamma_{40,50}$ increases monotonically with G for both cases (dashed line for homogeneous network or solid line for heterogeneous network). Therefore, stronger feedback gain is beneficial to synchronize the firing activity of the excitatory neurons.

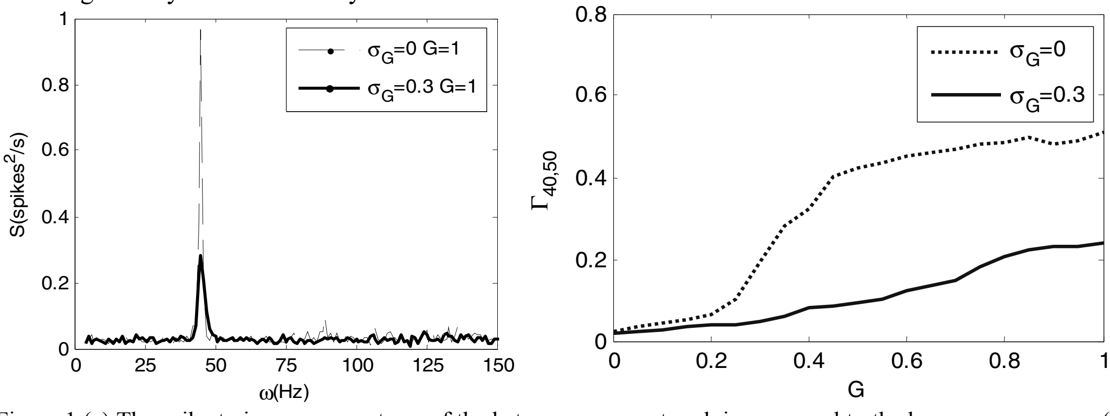

Figure 1 (a) The spike train power spectrum of the heterogeneous network is compared to the homogeneous case. (b) Relationship between the power of gamma oscillation and the inhibitory feedback gain in the heterogeneous network is compared to the homogeneous case.

In order to explore the robustness of the gamma oscillations, we calculate the spike train power spectrum of an excitatory neuron from the heterogeneous networks with varying σ_G . As shown in Fig.2, the heterogeneity in the feedback gain damages the gamma oscillations, leading to a decrease in height of the spectral peak. With the increase of σ_G, we obtain uniform power spectrums for heterogeneous networks with different values of G. The gamma oscillations are collapsed eventually due to heterogeneity, even if the inhibitory feedback is strong (G=0.7). Therefore, the global network oscillations are sensitive to high heterogeneity. In Fig.2, the spectral peak disappears for G=0.7 , when σ_G=0.5 . Nevertheless, the power spectrum is uniform for G=0.3 , when σ_G=0.2 . Stronger inhibitory feedback helps to improve the robustness of the gamma oscillations of the heterogeneous network. Furthermore, gamma oscillations can only be induced with small values of σ_G when the inhibitory feedback is weak. By strengthening the inhibitory feedback, the gamma oscillations are robust with a moderate amount of heterogeneity. Therefore, highly robust gamma oscillations can occur in heterogeneous networks with sufficiently strong inhibitory feedback.

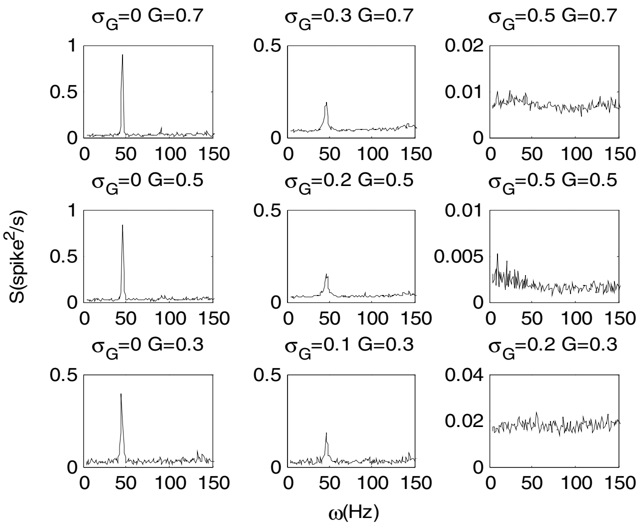

Figure 2 Power spectrums of an excitatory neuron from heterogeneous network

Finally, we study the relationship between the power of gamma oscillations and the standard deviation of heterogeneous noise. As illustrated in Fig.3, $\Gamma_{40,50}$ decreases inversely with σ_G . The vertical bars centered at the mean values are the standard deviations. The power of gamma oscillations keeps at high levels when $\sigma_G < 0.3$ and exhibits sharp deterioration after $\sigma_G > 0.3$. Therefore, the network can present drastic gamma oscillations when the degree of heterogeneity is controlled within a certain range. In this paper, the network oscillations can tolerate heterogeneous noise with standard deviation equaled to 0.3 , which is comparable to that observed in real neural systems.

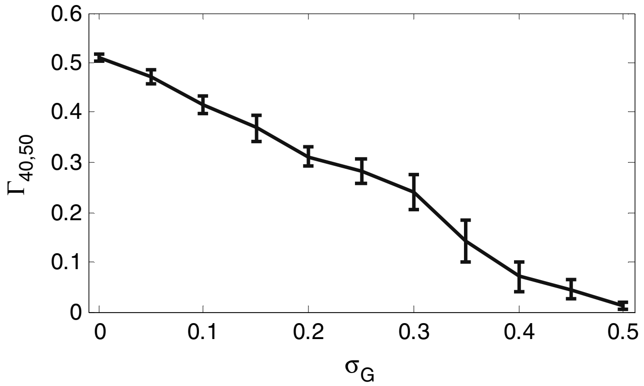

Figure 3 Relationship between the power of gamma oscillations and the standard deviation of heterogeneous noise.

4. Conclusion

Our simulation results show that the networks of excitatory and inhibitory neurons with inhibitory feedback loop exhibit gamma oscillations, which can be enhanced by strengthening the inhibitory feedback. In the presence of heterogeneity, neural firing rates are dispersed and synchronous rhythmic firing activity may break down. The gamma oscillations of our model are robust with a moderate amount of heterogeneity. However, the oscillatory activity deteriorates gradually with increasing heterogeneity. Sufficiently strong inhibitory feedback connections are critical to turn the heterogeneous networks into robust gamma oscillators. When inhibitory feedback is weak, the global network oscillations are sensitive to the heterogeneity. As the inhibitory feedback gain increases, the network oscillations develop a robust increasing tolerance against the heterogeneity, which is comparable to the degree of heterogeneity observed in real neural systems.

Acknowledgements

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References

[1] Ray, S., Niebur, E., Hsiao, S.S., Sinai, A., & Crone, N.E. High-frequency gamma activity (80-150Hz) is increased in human cortex during selective attention. *Clin. Neurophysiol. 2008, 119*, 116-133.

[2] Edwards, E., Soltani, M, Deouell, L.Y., Berger, M.S., & Knight, R.T. High gamma activity in response to deviant auditory stimuli recorded directly from human cortex. *J. Neurophysiol,2005. 94* , 4269–4280.

[3] Dong, Y., Mihalas, S., Qiu, F., von der Heydt, R., & Niebur, E. Synchrony and the binding problem in macaque visual cortex. *J. Vision 8*, 2008, 1–16.

[4] Miller, K.J., Leuthardt, E.C., Schalk, G., Rao, R.P., Anderson, N.R., Moran, D.W., Miller, J.W., & Ojemann, J.G.. Spectral changes in cortical surface potentials during motor movement. *J. Neurosci. 2007, 27*, 2424 –2432.

[5] de La Rocha, J., Doiron, B., Shea-Brown, E., Josic, K., & Reyes, A. Correlation between neural spike trains increases with firing rate. *Nature, 2007, 448,* 802-806.

[6] Gutnisky, D.A. & Dragoi, V. Adaptive coding of visual information in neural populations. *Nature, 2008, 452*, 220-224.

[7] Ecker, A.S., Berens, P., Keliris, G.A., Bethge, M., Logothetis, N.K., & Tolias, A.S. Decorrelated Neuronal Firing in Cortical Microcircuits. *Science, 2010, 327, 584-587.*

[8] Lindner, B., Doiron, B., & Longtin, A. Theory of oscillatory firing induced by spatially correlated noise and delayed inhibitory feedback. *Phys. Rev. E, 2005,72*, 061919.

[9] Renart, A., de la Rocha, J., Bartho, P., Hollender, L., Parga, N., Reyes, A., & Harris, K.D. The asynchronous state in cortical circuits. *Science. 2010, 327*, 587-590.

[10] Bartos, M., Vida, I., & Jonas, P. Synaptic mechanisms of synchronized gamma oscillations in inhibitory interneurons networks. *Nat. Rev. Neurosci.* 2007, *8*, 45-56.

[11] Wang, X.J. & Buzsaki, G. Gamma oscillation by synaptic inhibition in a hippocampal interneuronal network model. *J. Neurosci. 1996, 16*, 6402–6413.

[12] Marinazzo, D., Kappen, H.J., & Gielen, S.C.A.M. Input-driven oscillations in networks with excitatory and inhibitory neurons with dynamic synapses. *Neural Comput. 2007, 19,* 1739-1765.

[13] Borgers, C. & Kopell, N. Synchronization in networks of excitatory and inhibitory neurons with sparse, random connectivit. *Neural Comput. 2003, 15,* 509-538.